Response to selection for decreased backfat thickness at restrained intramuscular fat content in Duroc pigs[1]

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ABSTRACT: Intramuscular fat content (**IMF**) is a relevant trait for the pig industry and consumers. However, selection for IMF has the undesired correlated effect of decreasing lean growth. A selection experiment was performed to investigate the effects of selection against backfat thickness (**BT**) at restrained IMF. Barrows from a purebred Duroc line were allocated into a selected (n=165) or a control (n=185) group based upon their litter predicted EBV. Litters in the selected group were selected against BT at 180 d at restrained IMF in gluteus medius (**GM**) whereas those in the control group were chosen randomly. Realized selection intensities and genetic responses for BT, IMF in GM, and BW were estimated using a 3-trait multivariate animal mixed model under a Bayesian setting. Correlated responses for other traits were estimated similarly but using a 4-trait model, where other traits were added to the previous 3-trait model one at a time. Selected pigs had less BT than control pigs (-1.22 mm, with highest posterior density interval at 95% (HPD95) [-2.47; -0.75]) with restrained decrease in IMF, both in GM (-0.16%, HPD95 [-0.36; +0.05]) and in longissimus dorsi (-0.15%, HPD95 [-0.37; +0.09]). However, the realized selection intensity for IMF in GM denotes that the restriction on IMF was incomplete (-0.18, HPD95 [-0.36; +0.02]). Selection decreased BW (-1.64 kg, HPD95 [-2.47; -0.75]) but increased carcass lean weight (+0.66 kg, HPD95 [+0.14; +1.22]), indicating that the response in BT offsets the unfavorable correlated response in BW. Selected pigs were shorter (-0.50 cm, HPD95 [-0.81; -0.20]) but with similar ham weight and loin depth. These results provide evidence that lean weight can be improved restraining the genetic change in IMF. However, they also stress that a complete restriction on IMF is difficult to achieve unless selection is practiced on a big population where IMF is accurately predicted.

Key words: backfat thickness, growth, intramuscular fat, lean, pork, selection

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INTRODUCTION

Intramuscular fat content (**IMF**) is a key trait for marketing cured pork products, but it is also increasingly becoming relevant for fresh pork. Because IMF is unfavorably correlated with lean content, the selection for leanness undertaken in the last decades has led to develop genetic lines with a level of IMF that does not match the requirements of those specialized markets (Lonergan et al., 2001; Wood et al., 2008). However, the reported genetic correlations between lean-related traits and IMF are only moderate (Clutter, 2011), suggesting that there is room for improving lean growth independently from IMF.

Bosch et al. (2009, 2012) estimated the IMF content and backfat thickness (**BT**) at different age-points and muscles in a Duroc line. The values obtained by these authors proved that in some lines the problem is not IMF, which is already within the optimum range for dry-cured production, but overall fatness. Therefore, a suggestive breeding goal for such situations could be to increase leanness (reducing BT) subjected to minor change in IMF. It has been proved theoretically that this can be a feasible strategy (Solanes et al., 2009; Ros-Freixedes et al., 2012), but there is only little experimental evidence to support this approach. Results in the two experiments reported so far involving IMF in the selection objective (Suzuki et al., 2005a,b; Schwab et al., 2009, 2010) confirmed that IMF responds to selection, but also that selection for increased IMF is accompanied by increased overall fatness.

In this paper the results of a selection experiment conducted to investigate the effects of selection against BT at restrained IMF are presented.

MATERIALS AND METHODS

All experimental procedures were approved by the Ethics Committee for Animal Experimentation of the University of Lleida.

Selection Experiment

A selection experiment was conducted to study the effects of selection for decreased BT at restrained IMF. Selection was practiced in a purebred Duroc population that was completely closed in 1991 and since then it has been selected for an index including BW, BT, and IMF (Tibau et al., 1999). Selection was practiced among available litters at 4 established dates throughout 2006 and 2007 (selection batch 1 to 4). A litter born within 2 weeks before the set date was considered available for selection. In each batch, around 50 litters were allocated into a selected (**S**) or a control (**C**) group according to their litter (mid-parent) BLUP EBV for BT and IMF. Litters in group C were chosen randomly whereas those in group S were selected against BT at 180 d at restrained IMF in gluteus medius (GM). Linear programming was used to select the litters in group S. These litters were those with the lowest EBV for BT while satisfying the restriction of having the same mean EBV for IMF than the litters in group C (±0.03%). The EBV for BT and IMF were obtained from, respectively, 37,698 and 3,066 records at 180 d from full pedigree-connected pigs born since 1996. The IMF content was determined in GM by near infrared transmittance (**NIT**) spectrometry (Valero et al., 1999). The genetic evaluations were performed univariately using basically the same animal models described below (Solanes et al., 2009) but with heritabilities 0.19 and 0.40 for BT and IMF, respectively. Two males per litter were randomly chosen shortly after birth to be performance-tested according to the procedures indicated in the next section. The number of litters and pigs used in the experiment by selection group and batch is given in Table 1.

Management of Pigs and Sample Collection

The pigs in the experiment were castrated within the first week of age. At about 75 d of age piglets were moved to the fattening units, where they were penned (8 to 12 pigs/pen) until slaughter. Pigs from both groups were mixed and reared together. All pigs were performance-tested at an average age of 180 d for BW and BT. Backfat thickness was ultrasonically measured at 5 cm off the midline at the position of the last rib (Piglog 105, Herlev, Denmark). During the experiment pigs had ad libitum access to commercial diets. From 160 d onwards they were fed a commercial pelleted finishing diet (Esporc, Riudarenes, Girona, Spain) with an average composition of 16.3% crude protein, 6.7% fiber, and 6.8% fat. Feed in each batch was analysed in triplicate as described in Cánovas et al. (2009). At the end of the finishing period the barrows were slaughtered in a commercial slaughterhouse at 210 d of age.

After slaughter, the carcass weight (**CW**) and the carcass length were measured. The carcass length was measured from the anterior edge of the symphysis pubic to the recess of the first rib. Carcass BT and loin thickness at 6 cm off the midline between the third and fourth last ribs were measured by an on-line ultrasound automatic scanner (AutoFOM, SFK-Technology, Herlev, Denmark). The carcass lean percentage was estimated on the basis of 35 measurements of AutoFOM points by using the official approved equation (Decision 2001/775/CE, 2001) and the lean weight from CW and lean percentage. After chilling for about 24 h at 2ºC, each carcass was divided into primal cuts and the left side ham was weighed. Each ham was trimmed according to customary procedure used for manufacturing traditional dry-cured Spanish ham.

Immediately after quartering, a sample of at least 50 g of GM was taken from the ham, immediately vacuum packaged, and stored in deep freeze until required for IMF determination. A section of around 1 kg from the left loin of each carcass at the level of the third and fourth last ribs was also taken following the same procedure.

After the muscle samples were completely defrosted, vacuum drip losses were eliminated, and the dissected muscles, trimmed of subcutaneous and intermuscular fat, were minced. A representative aliquot from each pulverized freeze-dried muscle was used for fat analysis. The IMF content in GM and in LM was determined in duplicate by quantitative determination of the individual fatty acids by gas chromatography (Bosch et al., 2009). Fatty acid methyl esters were directly obtained by transesterification using a solution of 20% boron trifluoride in methanol (Rule, 1997). Methyl esters were determined by gas chromatography using a capillary column SP2330 (30 m × 0.25 mm, Supelco, Bellefonte, PA) and a flame ionization detector with helium as carrier gas. Runs were made with a constant column-head pressure of 172 kPa. The oven temperature program increased from 150 to 225ºC at 7ºC/min and injector and detector temperatures were both 250ºC. The quantification was carried out through area normalization after adding into each sample 1,2,3-tripentadecanoylglycerol as internal standard. Intramuscular fat content was calculated as the sum of each individual fatty acid expressed as triglyceride equivalents (AOAC, 1997).

Analysis of Response to Selection

The response to selection was estimated as the difference between the average EBV of the pigs in group S and the pigs in group C. A description of the selection groups by batch is given in Table 1. The genetic parameters and EBV of the pigs for BT, IMF in GM, and BW were estimated fitting a 3-trait multivariate animal model under a Bayesian setting, in line with the methodology described in Ros-Freixedes et al. (2012). The genetic parameters and EBV of other correlated traits were obtained using a 4-trait model, where each of them was added one at a time to the previous 3-trait model. A summary of the data used for the analyses is given in Table 2. Records for BT and BW were collected in pigs born from 1996 to 2009 while carcass traits only in pigs born since 2002 onwards.

The model used was:

$$y_i = X_i b_i + Z_i a_i + W_i c_i + e_i ,$$

where $\mathbf{y}_i$ is the vector of observations for the ith trait; $\mathbf{b}_i$, $\mathbf{a}_i$, $\mathbf{c}_i$, and $\mathbf{e}_i$ are the vectors of systematic, additive genetic, litter, and residual effects, respectively; and $\mathbf{X}_i$, $\mathbf{Z}_i$, and $\mathbf{W}_i$, the known incidence matrices that relate $\mathbf{b}_i$, $\mathbf{a}_i$, and $\mathbf{c}_i$ with $\mathbf{y}_i$, respectively. Systematic effects for BW and BT were the batch (1039 levels), gender (3 levels; males, females, and castrates), and age at test as a covariate. Pigs tested at the same time and in the same unit were considered as one batch. The model for the other traits only included the batch (12 levels) and the age at slaughter. The litter effect was not included in the model for carcass traits because there were only 1.7 piglets with these data per litter.

The genetic parameters and EBV for all traits were estimated in a Bayesian framework using Gibbs sampling with the TM software (Legarra et al., 2008). The traits were assumed to be conditionally normally distributed as follows:

$$\begin{bmatrix} y_1 \\ y_2 \\ y_3 \\ y_4 \end{bmatrix} | \ \mathbf{b}_1, \mathbf{b}_2, \mathbf{b}_3, \mathbf{b}_4, \mathbf{a}_1, \mathbf{a}_2, \mathbf{a}_3, \mathbf{a}_4, \mathbf{c}_1, \mathbf{c}_2, \mathbf{R} \sim \mathrm{N}\left(X \begin{bmatrix} b_1 \\ b_2 \\ b_3 \\ b_4 \end{bmatrix} + Z \begin{bmatrix} a_1 \\ a_2 \\ a_3 \\ a_4 \end{bmatrix} + W \begin{bmatrix} c_1 \\ c_2 \end{bmatrix}, R \right),$$

where **R** was the (co)variance matrix. Sorting records by pig, and trait within pig, **R** could be written as $\mathbf{R}_0 \otimes \mathbf{I}$, with $\mathbf{R}_0$ being, in the most general case, the 4 × 4 residual (co)variance matrix between the four traits analyzed and **I** an identity matrix of appropriate order. Flat priors were used for $\mathbf{b}_i$ and residual (co)variance components. Additive genetic and litter values, conditionally on the associated (co)variance components, were both assumed multivariate normally distributed with mean zero and with (co)variance $\mathbf{G} \otimes \mathbf{A}$ and $\mathbf{C} \otimes \mathbf{I}$, respectively, where **A** was the numerator relationship matrix, **G** was the 4 × 4 genetic relationship matrix between the four traits, and **C** was the 2 × 2 (co)variance matrix between litter effects of BW and BT. The matrix **A** was calculated using all the pedigree information summarised in Table 2. Flat priors were used for additive and litter (co)variance components. Statistical inferences for all unknowns were derived from the samples of the marginal posterior distribution using a unique chain of 1,000,000 iterations, where the first 250,000 were discarded and one sample out of 100 iterations retained. Statistics of marginal posterior distributions and the convergence diagnostics were obtained using the BOA package (Smith, 2005). Convergence was tested using the *Z*-criterion of Geweke (Geweke, 1992) and visual inspection of convergence plots.

The response to selection for the *i*th trait ($\mathbf{R}_{(i)}$) was calculated as:

$$R_{(i)}=\acute{a}_{S(i)}-\acute{a}_{C(i)},$$

where $\bar{a}_{S(i)}$ and $\bar{a}_{C(i)}$ are the average of the EBV for the *i*th trait in pigs from group S and C, respectively. Overall responses to selection and by batch were calculated. In this latter case only the pigs from the corresponding batch were used in the above expression. The realized selection intensities for BT and IMF in GM (**$i_{S(i)}$** and **$i_{C(i)}$**, for the *i*th trait and group S and C, respectively) were obtained by calculating the standardized selection differentials as follows:

$$i_{S(i)} = (\acute{a}_{S(i)} - \acute{a}_{all(i)})/\sigma_{a(i)}$$

and

$$i_{C(i)} = (\acute{a}_{C(i)} - \acute{a}_{all(i)})/\sigma_{a(i)}$$

where $\bar{a}_{all(i)}$ is the average EBV of pigs from all candidate litters (i.e., available litters at each selection time-point) for the *i*th trait; and $\sigma_{a(i)}$ the genetic standard deviation of the trait. Both $i_{S(i)}$ and $i_{C(i)}$ were calculated independently for each batch, with the EBV obtained using only the data collected up to the selection time-point of the batch. The average realized selection intensity of the experiment was calculated weighting the realized selection intensity across the four batches. Statistical inferences for genetic parameters, realized selection intensities, and responses to selection were derived from random samples of the corresponding marginal posterior distributions. In particular, the mean, the mode, the SD, and the highest posterior density interval at 95% (**HPD95**) of the marginal posterior distributions were calculated. Response to selection was assessed using the HPD95 and the probability of $R_{(i)}$ being negative.

RESULTS

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Genetic Parameters

Estimates of the variance components and the heritability for each of the analyzed traits, as well as the genetic and residual correlations of BT, IMF in GM, and BW with carcass traits and IMF in LM are given in Table 3. The estimates of the heritability were within the expected range, from 0.31 (SD 0.01), for BW, to 0.69 (SD 0.09), for IMF in LM. The genetic correlations of BT with carcass traits were positive, except for the lean-related traits loin thickness (-0.40, SD 0.13), lean percentage (-0.88, SD 0.04), and lean weight (-0.49, SD 0.08). A similar genetic correlation structure was found for IMF in GM but, in general, lower in magnitude. The genetic correlations of IMF in GM with carcass loin thickness (-0.58, SD 0.07), lean percentage (-0.45, SD 0.11), and lean weight (-0.38, SD 0.12) were also negative. However, for IMF in GM, the genetic correlation with ham weight was much lower (0.09, SD 0.16) than for BT (0.36, SD 0.09). The genetic correlation of BT with IMF, both in GM (0.38, SD 0.10) and in LM (0.41, SD 0.12) was lower than observed between IMF in GM and LM (0.64, SD 0.10).

Realized Selection Intensities

The realized selection intensities are given in Table 4. As expected, in group S, the overall realized selection intensity for BT was negative (-0.49, HPD95 [-0.62, -0.35]) whereas that for IMF in GM was much closer to zero (-0.18, HPD95 [-0.36, +0.02]). By contrast, the values in group C confirmed that pigs in this group were randomly chosen both for BT (+0.09, HPD95 [-0.03, +0.21]) and IMF in GM (0.00, HPD95 [-0.15, +0.15]). The corresponding realized selection differentials were -0.93 mm (HPD95 [-1.18,-0.67]); -0.25% (HPD95 [-0.53, +0.02]); +0.17 mm (HPD95 [-0.06, +0.40]); and 0.00% (HPD95 [-0.23, +0.21]), respectively. These results were consistent across the four selection batches. The associated HPD95 indicate that selection for BT was effective in all batches, but also that the constraint imposed on IMF was not fully accomplished.

Direct Response to Selection

The phenotypic values of BT and IMF in GM by selection group and batch are given in Table 1. The features of the posterior distribution of the direct response to selection on these traits are given in Table 5. Selection against BT was effective (the probability of $R_{(BT)}$ being negative was greater than 0.99 in all batches), with an overall reduction of 1.22 mm (HPD95 [-1.51, -0.93]). The results also indicated that selection was not completely neutral with respect to IMF in GM. The IMF content in GM showed an overall decrease of 0.16% (HPD95 [-0.36, +0.05]), with a probability of 94% of getting a negative response. However, this probability was lower within each selection batch, where it ranged from 72 to 88%.

Correlated Response to Selection

The features of the posterior distribution of the correlated responses are given in Table 6. Selection reduced BW (-1.64 kg, HPD95 [-2.47, -0.75]), CW (-1.83 kg, HPD95 [-2.71, -0.85]), and carcass length (-0.50 cm, HPD95 [-0.81, -0.20]), whereas it increased lean percentage (+1.47%, HPD95 [+0.98, +1.97]). The favorable response in lean percentage more than offset the unfavorable correlated response in CW, thereby resulting in a favorable correlated response in carcass lean weight (+0.66 kg, HPD95 [+0.14, +1.22]). Despite the loss in CW, no correlated change in ham weight was detected. The correlated response in IMF in LM was similar to that in GM (-0.15%, HPD95 [-0.37, +0.09]), but with a lower probability of being negative (90%). In general, the overall correlated responses were consistent across selection batches

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(results not shown). Nonetheless, in this regard it is worth noting that in batch 2 there was found a relatively high probability (82%) of a positive response in IMF in LM, a result proving that there exist scenarios where BT and IMF can be improved simultaneously.

DISCUSSION

The selection experiments undertaken so far for increased IMF proved that IMF responds to selection but at the expense of increasing BT (Suzuki et al., 2005a,b; Schwab et al., 2009, 2010). Previous theoretical studies using the estimates of the genetic parameters obtained in this population showed that, despite the positive genetic correlation between BT and IMF, there are response scenarios where BT can be reduced with no change in IMF (Solanes et al., 2009; Ros-Freixedes et al., 2012). The results presented here confirmed experimentally that such goal is feasible but difficult. Thus, even though the response in IMF was restrained, there is not compelling evidence that the constraint had been fully achieved.

The expected correlated response in IMF to one generation of unrestricted selection against BT can be approached as (Falconer and Mackay, 1996):

$$R_{(IMF)} = r_{g(IMF,BT)} \frac{\sigma_{a(IMF)}}{\sigma_{a(BT)}} R_{(BT)},$$

where $r_{g(IMF,BT)}$ is the genetic correlation between BT and IMF. In such situation, with the genetic parameters given in Table 4, decreasing BT by 1.22 mm is expected to result in a correlated reduction in IMF of 0.30%, in GM, and of 0.26%, in LM, values that are

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around 2-fold those realized. Therefore, in practical terms, the imposed restriction on IMF served to halve the correlated response in IMF. That the restriction had not been fully effective is in line with the negative value of the realized selection differential for IMF in the selected group. A reason for that could be the poor predictive capacity of the mid-parent EBV for IMF used for selection. It can be retrospectively assessed by correlating the litter EBV with the phenotypic values of the offspring. This correlation was 0.12, for IMF, and 0.27, for BT, and increased to 0.20 and 0.34, respectively, for the realized EBV, which were calculated using the multivariate model and data used for estimating the realized selection intensities. These predictive capacities are consistent with the precision of the EBV in the experimental pigs, calculated as 1 - $\sigma^2_{EBV}/\sigma^2_e$, where σ^2_{EBV} is the variance of the EBV of an individual between iterations and σ^2_e the residual variance of the corresponding trait. The average precisions were 0.45 (0.33 to 0.50), for IMF, and 0.62 (0.47 to 0.64), for BT. These results explain why selection response for lower BT was more successful than the restriction on IMF. Moreover, they evidenced that there is scope for improvement. In fact, although retrospectively, it can be proved that there is a subset of 90 barrows in group S showing, as compared to pigs in group C, much lower BT (-1.79 mm, HPD95 [-2.13, -1.44]) but identical IMF in GM (0.00%, HPD95 [-0.28, +0.28]). This result highlights the fact that selection against BT does not necessarily lead to decrease IMF if accurate EBV for IMF are available and the population is big enough to allow the pigs with low BT and high IMF to be sorted out.

The selected pigs were lighter and had lighter carcasses. Because BW is shown to be genetically more correlated to BT than to IMF (Table 4), selection for BT is expected to cause greater changes in BW than selection for IMF. This is in line with results from the experiments in Schwab et al. (2009, 2010), who found no correlated response in growth performance to selection for IMF, and in Solanes et al. (2009), who showed in this population that selection for BW at restrained BT did not affect IMF. Results from commercial lines suggest that changes in IMF depend on the selection emphasis that has been put on growth as compared to lean content, with pigs that had been more intensively selected for daily gain than for lean content showing higher IMF (Oksbjerg et al., 2000; Tribout et al., 2004). In this regard, carcass lean weight is a more appropriate trait for the industry (Fowler et al., 1976; Chen et al., 2002, 2003). Lighter carcasses at a fixed age mean that there has been a loss in either fat or lean mass or both during the fattening period. The results here support the hypothesis that decreased CW is mostly due to fat loss. The selected pigs not only increased carcass lean weight, but also they were able to decrease carcass BT without adversely affecting loin thickness. Thus, the detrimental effect of selection on CW (BW) becomes less relevant when expressed in terms of lean growth. This is in line with the findings in Gjerlaug-Enger et al. (2012), who in a recent study on body composition using computerized tomography found that the genetic variation in carcass lean percentage is more determined by fat than by muscle growth. No data on feed intake was available for this research, but feed efficiency is known to be negatively correlated to fatness. Some authors reported a similar genetic correlation of feed efficiency with both BT and IMF (Hermesch et al., 2000; Cai et al., 2008) while others found it more correlated to BT than to IMF (Suzuki et al., 2005b). In either case, the selected pigs should be at least as efficient as the control.

The two more important retail pork cuts are ham and loin, particularly for the dry-cured market. Even though the relationship between fatness and carcass quality can be negligible in light white pigs (Hermesch et al., 2000), the correlation pattern observed here between BT and IMF with ham weight, loin thickness, and carcass length, together with previously reported estimates in Iberian (Fernández et al., 2003) and Duroc

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(Suzuki et al., 2005a; Solanes et al., 2009) heavy pigs, indicate that selection against fatness may lead to undesired effects on primal cuts. However, in terms of correlated responses, side effects were only found in carcass length, but not in ham weight and loin thickness, thereby suggesting that the loin may be more sensitive than the ham to simultaneous selection for BT and IMF. The results of our selection experiment indicate that selection for BT at restrained IMF may lead to shorter (lower carcass length), but not narrower (loin thickness did not decrease) loins, in agreement with the positive genetic correlation observed between BT and carcass length, both here and elsewhere (Johnson and Nugent, 2003; Chimonyo and Dzama, 2007). These results contradict the findings in Schwab et al. (2009), who found that selected pigs for increased IMF had lower loin muscle area but similar carcass length. However, it is worth noting that in this latter experiment BW did not significantly change by selection. Because the weight of primal cuts greatly depends on BW, their correlated responses must be interpreted in light of the correlated changes observed in BW.

The metabolism of IMF may differ among muscles (Sharma et al., 1987; Leseigneur-Meynier & Gandemer, 1991; Muriel et al., 2002) and even among locations within muscle (Sharma et al., 1987). The molecular mechanisms of the differential deposition patterns are not well known, and therefore it still remains uncertain whether changes in a muscle cause correlated changes into another. Most research so far concerning IMF in pigs used LM as the reference muscle. However, neither LM is the only valuable muscle nor likely, because of depreciation costs, it is the most convenient for sampling purposes. In this experiment GM has been used as the reference muscle for determining IMF. It has been shown that IMF in LM is not only highly genetically determined, but also that it displays a high genetic correlation with IMF in GM. Therefore, the correlated response for IMF in LM was very similar to that for IMF in

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GM. While this is a comforting outcome of the experiment, it needs to be assessed in other muscles differing in IMF content and fiber composition.

In conclusion, the results of the present selection experiment provide evidence that lean weight can be improved restraining the genetic change in IMF, both in GM and LM. The selection practiced may lead to lighter pigs, mainly due to decreased body fat rather than lean. Nonetheless, attention should be paid to primal cuts, which can be lighter too. Simultaneous genetic improvement of BT, IMF, and BW should be feasible if the accuracy of the EBV for IMF, along with the selection intensity, is high enough. While accuracy for IMF can be easily increased with a well-designed recording scheme, selection intensity may be a problem in small populations. The experimental design used here was based on a series of one-generation selection batches aimed at proving that BT and IMF can be manipulated independently. Selecting for more traits would have reduced the response in BT and therefore the power of the experiment. However, in practice, pigs are continuously selected across generations for an objective including all relevant traits. Short-term responses are lower, but in the long-term the population can be better accommodated to specific needs.

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Table 1. Number of pigs, litters, and sires, and mean (SD) of backfat thickness (BT) at 180 d, intramuscular fat (IMF) in gluteus medius (GM), and BW at 180 d by selection group and batch

Selection group	No. of pigs	No. of litters	No. of sires	Traits		
				BT, mm	IMF in GM, %	BW, kg
Batch 1						
Selected	55	31	12	17.89 (3.98)	4.32 (2.23)	99.52 (12.94)
Control	52	30	19	19.54 (5.10)	4.50 (2.05)	101.37 (17.93)
Batch 2						
Selected	47	30	14	16.77 (3.21)	4.72 (2.79)	104.50 (9.87)
Control	58	31	20	17.09 (3.54)	4.78 (2.33)	104.82 (10.41)
Batch 3						
Selected	30	22	12	16.45 (2.25)	4.74 (2.42)	105.92 (9.40)
Control	36	24	14	19.22 (3.28)	4.89 (2.94)	109.95 (9.44)
Batch 4						
Selected	33	20	9	14.38 (2.89)	3.36 (1.43)	105.18 (14.08)
Control	39	23	10	16.05 (2.96)	3.71 (1.99)	113.87 (11.23)

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497**Table 2.** Description of the data set used in the analysis of the response to selection

Item	No. of pigs	No. of litters	No. of sires	No. of dams	Mean	SD
Pedigree	93,920	32,315	731	18,516	-	-
Traits[1]						
BT at 180 d, mm	80,687	31,197	642	16,335	15.6	3.5
IMF in GM, %	943	546	141	543	4.9	1.9
BW at 180 d, kg	85,002	32,211	641	16,548	104.8	12.5
Carcass weight, kg	937	545	142	542	98.4	11.6
Carcass length, cm	446	270	85	270	86.8	3.0
Carcass BT, mm	921	538	142	535	23.4	3.8
Carcass loin thickness, mm	921	538	142	535	43.7	7.9
Carcass lean percentage, %	921	538	142	535	42.9	5.2
Carcass lean weight, kg	920	538	142	535	42.0	5.7
Ham weight, kg	431	268	85	268	12.1	1.2
IMF in LM, %	189	149	65	149	3.9	1.2
Covariates						
Age at test , d	85,194	32,310	642	16,601	180.2	10.7
Age at slaughter, d	2,098	1,370	298	1,313	206.5	14.6

498[1]BT: backfat thickness; IMF in GM (LM): intramuscular fat in gluteus medius
499(longissimus dorsi).

Table 3. Posterior means (SD) of variance components (σ_a^2: additive genetic, σ_e^2: residual) and heritability (h^2) of all analyzed traits, and genetic (r_g) and residual (r_e) correlations of backfat thickness (BT) at 180 d, intramuscular fat (IMF) in gluteus medius (GM), and BW at 180 d with other carcass traits

	Variance components			r_g			r_e		
Trait	σ_a^2	σ_e^2	h^2	BT	IMF in GM	BW	BT	IMF in GM	BW
BT	4.11 (0.61)	4.44 (0.08)	0.45 (0.01)	-	0.38 (0.10)	0.63 (0.02)	-	0.14 (0.08)	0.60 (0.01)
IMF in GM	1.77 (0.31)	1.45 (0.23)	0.55 (0.08)	0.38 (0.10)	-	0.28 (0.10)	0.14 (0.08)	-	0.06 (0.07)
BW	29.76 (1.34)	57.23 (0.78)	0.31 (0.01)	0.63 (0.02)	0.28 (0.10)	-	0.60 (0.01)	0.06 (0.07)	-
Carcass traits									
Weight	39.77 (4.22)	47.89 (3.30)	0.45 (0.04)	0.59 (0.05)	0.17 (0.11)	0.96 (0.02)	0.58 (0.03)	0.14 (0.09)	0.88 (0.01)
Length	5.05 (0.91)	3.72 (0.63)	0.57 (0.08)	0.27 (0.11)	0.22 (0.15)	0.70 (0.08)	0.29 (0.08)	-0.07 (0.15)	0.76 (0.05)
Carcass BT	6.73 (0.97)	5.66 (0.70)	0.54 (0.06)	0.91 (0.03)	0.36 (0.10)	0.61 (0.06)	0.48 (0.04)	0.20 (0.10)	0.32 (0.05)
Loin thickness	19.77 (4.37)	41.05 (3.77)	0.32 (0.06)	-0.40 (0.13)	-0.58 (0.13)	0.04 (0.13)	0.05 (0.07)	0.14 (0.11)	0.14 (0.06)
Lean percentage	13.00 (1.92)	10.21 (1.37)	0.56 (0.07)	-0.88 (0.04)	-0.45 (0.11)	-0.50 (0.07)	-0.36 (0.05)	-0.11 (0.12)	-0.18 (0.06)
Lean weight	12.34 (2.23)	14.14 (1.66)	0.46 (0.07)	-0.49 (0.08)	-0.38 (0.12)	0.18 (0.09)	0.23 (0.06)	0.05 (0.11)	0.62 (0.05)
Ham weight	0.49 (0.09)	0.71 (0.07)	0.41 (0.06)	0.36 (0.09)	0.09 (0.16)	0.83 (0.06)	0.46 (0.05)	0.03 (0.11)	0.87 (0.03)
IMF in LM	1.11 (0.20)	0.49 (0.15)	0.69 (0.09)	0.41 (0.12)	0.64 (0.10)	0.14 (0.15)	0.24 (0.15)	0.19 (0.18)	0.25 (0.15)

Table 4. Realized selection intensity for backfat thickness (BT) at 180 d and intramuscular fat (IMF) in gluteus medius (GM) by selection group

Selection group	BT		IMF in GM	
	Mean	HPD95[1]	Mean	HPD95[1]
Average				
Selected	-0.49	-0.62; -0.35	-0.18	-0.36; +0.02
Control	+0.09	-0.03; +0.21	0.00	-0.15; +0.15
Batch 1				
Selected	-0.40	-0.62; -0.20	-0.17	-0.51; +0.17
Control	+0.16	-0.05; +0.38	-0.05	-0.33; +0.23
Batch 2				
Selected	-0.45	-0.69; -0.23	-0.13	-0.45; +0.16
Control	+0.08	-0.12; +0.27	+0.03	-0.21; +0.29
Batch 3				
Selected	-0.40	-0.69; -0.10	-0.14	-0.52; +0.22
Control	+0.18	-0.09; +0.44	+0.10	-0.24; +0.45
Batch 4				
Selected	-0.76	-1.11; -0.39	-0.27	-0.77; +0.24
Control	-0.07	-0.33; +0.23	-0.06	-0.46; +0.32

[1]HPD95: highest posterior density interval at 95%.

Table 5. Features of the posterior distribution of the response to selection to decreased backfat thickness (BT) at 180 d at restrained intramuscular fat content (IMF) in gluteus medius (GM)

	Response				
Trait	Mean	SD	Mode	HPD95[1]	*P* <0[2]
BT, mm					
Overall	-1.22	0.15	-1.26	-1.51; -0.93	>0.99
Batch 1	-1.35	0.26	-1.37	-1.89; -0.85	>0.99
Batch 2	-0.76	0.26	-0.67	-1.27; -0.23	>0.99
Batch 3	-1.55	0.33	-1.55	-2.20; -0.91	>0.99
Batch 4	-1.43	0.32	-1.39	-2.07; -0.82	>0.99
IMF in GM, %					
Overall	-0.16	0.10	-0.15	-0.36; +0.05	0.94
Batch 1	-0.11	0.18	-0.12	-0.45; +0.25	0.74
Batch 2	-0.10	0.17	-0.07	-0.44; +0.24	0.72
Batch 3	-0.21	0.23	-0.18	-0.67; +0.24	0.82
Batch 4	-0.27	0.23	-0.31	-0.70; +0.19	0.88

[1]HPD95: highest posterior density interval at 95%.

[2]Probability of having a negative response.

Table 6. Features of the posterior distribution of the overall correlated responses to selection to decreased backfat thickness (BT) at 180 d at restrained intramuscular fat content (IMF) in gluteus medius

	Response				
Trait	Mean	SD	Mode	HPD95[1]	*P* <0[2]
BW, kg	-1.64	0.44	-1.76	-2.47; -0.75	>0.99
Carcass traits					
Weight, kg	-1.83	0.47	-1.73	-2.71; -0.85	>0.99
Length, cm	-0.50	0.16	-0.42	-0.81; -0.20	>0.99
Carcass BT, mm	-1.15	0.19	-1.18	-1.51; -0.78	>0.99
Loin thickness, mm	+0.48	0.45	0.31	-0.41; +1.34	0.14
Lean percentage, %	+1.47	0.25	+1.51	+0.98; +1.97	<0.01
Lean weight, kg	+0.66	0.27	+0.62	+0.14; +1.22	0.01
Ham weight, kg	-0.07	0.06	-0.06	-0.18; +0.05	0.87
IMF in LM, %	-0.15	0.12	-0.10	-0.37; +0.09	0.90

[1]HPD95: highest posterior density interval at 95%.

[2]Probability of having a negative response.